ECOLOGISCHE WAARNEMINGEN AAN AMFIBIEËN

j. j. van gelder

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PROMOTOR:

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PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE
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Nijmegen

Figuur op de omslag:

Gouden sieraad, meer dan vijf eeuwen geleden vervaardigd door indianen van centraal Amerika. De kikker verwelkomt met zijn gezang de regen die mens en land verkwikt.

tekening van J. Gerritsen naar een foto in National Geographic, juli 1973

INHOUD

PUBLICATIES

TEN GELEIDE

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ECOLOGICAL OBSERVATIONS ON AMPHIBIA IN THE NETHERLANDS

I. RANA ARVALIS NILSSON: REPRODUCTION, GROWTH, MIGRATION AND POPULATION FLUCTUATIONS

by

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CONTENTS

I. INTRODUCTION

In Europe most species of Amphibia are locally abundant, but for most of them a full account of their ecology is still lacking. Even from the period of reproduction of Anura data are incomplete, although field observations are considerably facilitated by a gregarious mode of reproduction.

The extensive investigations on the ecology and life history of the common frog by SAVAGE (1961) in Great Britain have resulted in a unique position of *Rana temporaria* L. This author gives a wealth of

information, *e.g.*, on development, breeding behaviour, hibernation and migration. RÜHMEKORF (1958) gives some information on spawning sites and temperatures at spawning places of Anura in Germany. GISLÉN & KAURI (1959) mention for Sweden the time of spawning, length of larval period and body-length of different year classes. ZIMKA (1966) and MAZUR (1966) studied selection of food by *Rana arvalis*.

In 1961–1963 we observed big populations of several species of Amphibia in "de Hamert" (property of "Het Limburgs Landschap"). Three species occurred in sufficient numbers for population studies: *Rana arvalis* Nilsson, *Rana esculenta* L. and *Triturus helveticus* Raz. The following species were also present in this area: *Pelobates fuscus* Laur.,

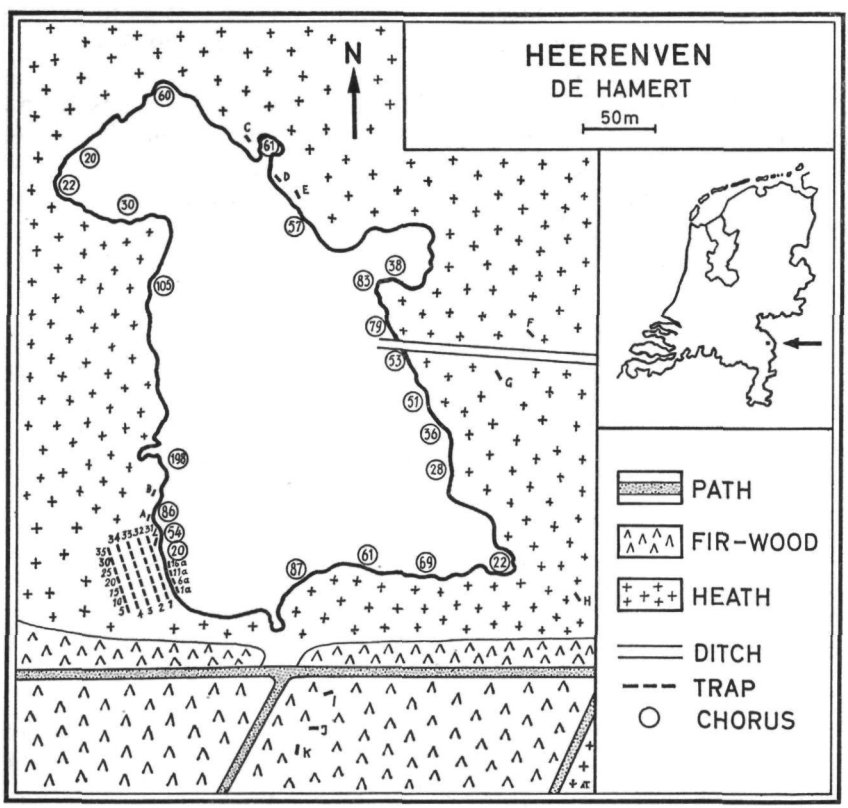

Fig. 1. Experimental area "Heerenven". Inset map of the Netherlands shows location. Traps 1–35 situated in trapping-square, a-l situated around "Heerenven". Circles mark places where choruses were observed in 1968; figures mean the number of egg clumps in that year.

Bufo bufo L., *Bufo calamita* Laur., *Triturus vulgaris* L. and *Triturus cristatus* Laur.

This paper deals with *Rana arvalis* Nilsson; it presents data on reproduction, growth, migration and fluctuations in the population during 1964–1968.

II. DESCRIPTION OF THE AREA

"De Hamert" is located in the north of the province of Limburg (51.30 'N, 6.10 'E, Fig. 1); it is an area of inland dunes with scattered ponds (Dutch: "vennen").

In spring *Rana arvalis* concentrates in one of these ponds ("Heerenven", Fig. 1). The water level of the Heerenven depends on precipitation, some drainage from cultivated lands (ditch, Fig. 1), and on evaporation and seepage through the bottom.

During 1964–1968 the greatest difference in water level was 1.5 m. Fluctuations in water level had considerable influence on the size of the water surface: Fig. 1 represents the average situation with greatest depth of 1.2 m. The character of the water varied with the level as indicated by two samples in Table I.

TABLE I

Some physico-chemical data of the water at different water levels.

level	*pH*	*Cl'-ppm*	*O_2-ppm*	*O_2% saturation*
low	7.4	21.0	2.83	31.7
high	5.4	13.5	8.50	92.5

Polygonum amphibium grows in the water, *Scirpus lacustris*, *Carex rostrata*, *Juncus effusus* and *Hydrocotyle vulgaris* on the border, *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea* on a somewhat higher level.

III. METHODS

From 1964 on the area was visited once or twice a week except for three months in the summer of 1967. Observations were made on the formation of the breeding choruses and the spawning and the development of the eggs. The greater part of the data on locomotory activity was obtained by means of traps. These are wooden boxes with length $\times$ width $\times$ depth $= 60 \times 25 \times 40$ cm, arranged with their long axis parallel to the water line. Most of the traps were arranged in a rec-

tangular pattern ("trapping-square") on the west side of the Heerenven (see Fig. 1), the distance between the boxes being 10 meters. During the investigation the number of traps was enlarged to get a better yield of frogs. In 1964 the initial number was 24 (1a–20, Fig. 1), in 1965 12 boxes were dug in around the Heerenven (A-L, Fig. 1), in 1968 the original trapping-square was enlarged with 15 boxes (21–35, Fig. 1). In spring 1966 and 1967 a part of these was flooded and could not be used.

In the traps frogs survived very well and could not escape. Frogs were measured (length of snout to urostyl), sexed and released afterwards at a well determined location between the traps.

IV. RESULTS

A. *Direct observations*

1. *Copulation and spawning*

Only at the time of reproduction *Rana arvalis* could be found in the water. Breeding choruses were restricted to a very short period in early spring. During this period choruses of males could be recorded in shallow (20 cm) sunny places all along the edge of the pond. Fig. 1 gives the sites of the choruses in 1968. As a rule within a few days mating began and eggs were deposited. Immediately afterwards amplexuses were terminated. During about three days two marked scars remained visible in the skin of the females on both sides of the sternum. This phenomenon, caused by the warts on the thumbs of the males, has never been described. Eggs were laid in rounded clumps. The number of eggs in a clump varied from 800 to 1,200. In Fig. 1 the number of clumps per chorus in 1968 is indicated. In this year the total number of eggs amounted to about 1,300,000.

The following data are taken from our records:

19–3–1968: First amplexus.
22–3–1968: One clump found; four pairs in amplexus.
24–3–1968: Five clumps present; six pairs in amplexus; no chorus recorded.
26–3–1968: Breeding choruses are present in several places (Fig. 1); number of clumps: 750.
29–3–1968: Number of clumps about 1,300; choruses no longer present.

After 29–3–1968 no new clumps have been found. In 1964, 1965, 1966 and 1968 the main spawning fell on April 2, March 31, March 10

and March 26, respectively. The average temperature of the day on these dates was 4, 9, 5 and 10° C.

2. *Development until metamorphosis*

The duration of the larval period varied in different years, as is shown in Table II.

This table shows that the influence of the temperature on the length of larval life cannot be excluded. During all the years of observation the whole larval population of the Heerenven completed its metamorpho-

TABLE II

Duration of larval life in weeks and characteristics of temperature in April, May and June according to K.N.M.I. (Royal Dutch Meteorologic Institute) in four years.

year	*larval period*	*temperature*
1964	11	above normal*
1965	15	below normal
1966	14	normal
1968	13	normal

* Normal means: there is no difference between the average day temperature as compared with the average day temperature of the same period during 1931–1960.

sis within one week. The tail of a young frog was resorbed within two days. It could be observed that with decreasing water level in 1964 a certain number of egg clumps dried out at the border of the water. Moreover, throughout the entire period of observation a part of the egg clumps was infected with a fungus.

B. *Results by means of traps*

During the five years of observation a total number of 2,203 frogs was caught. A synopsis of length, sex and date of capture is presented in Fig. 2.

Frogs were trapped in greatest numbers during early spring. These samples contained specimens measuring 40–60 mm. Individuals measuring 25–30 mm were also found. Only specimens with a length above 40 mm could be sexed with certainty. It must be emphasized that during June and July a considerable part of the youngest frogs has been caught by hand in the vicinity of the water. Even then they were only caught if they showed locomotory activity, as the adults do when

they are trapped. For this reason these youngest frogs are put in Fig. 2 as well, although trapping and catching by hand are different methods. In Fig. 2 the years 1964, 1965 and 1968 show the same picture. Spring 1966 and spring 1967 differ from the other years; this is due to flooding of most of the traps which resulted in a small yield of frogs.

1. *Length in relation to age*

a. First year frogs

Specimens of 15–19 mm have just metamorphosed. The length of these young frogs differed only slightly in four years. Fig. 2 shows how these young frogs grew: at the end of the season they had a length of 20–34 mm.

b. Second year frogs

Individuals are called second year frogs after their first hibernation. The length of second year frogs at the beginning of the season was equal to the length of the first year frogs at the end of the past season (21–33 mm). Thus in winter they do not increase in length (compare, for example, the length of first year frogs at the end of 1965 with the length of second year frogs at the beginning of 1966).

At the end of the season most of the second year frogs had reached a length of more than 40 mm; at that time it was possible to distinguish males from females.

c. Adults

At the end of the season it was no longer possible to distinguish between fast grown second year frogs and slowly grown third year specimens. From this moment on we were not able to discern year classes.

Lengths of adults varied from about 40 to about 65 mm (largest male 65 mm, largest female 69 mm). However, the difference in average length between sexes was only slight. There was neither a difference in average length of adults in successive years. The relatively small numbers of frogs caught in 1966 and 1967, due to flooding of considerable numbers of traps during spring, may be a cause of slight deviation.

Always more females than males were found. The sex ratios in 1964, 1965 and 1968 were equal (Table III). The deviation in 1966 and 1967 may be caused also by flooding of traps. The mean sex ratio for the five years was 0.67.

TABLE III

Survey of the catches. Length, sex ratio and total numbers of adults. Length in mm.

Year of observation	*First year frogs length-range*		*Second year frogs length-range*		*Adults average length*			
	after metamorphosis	*before hibernation*	*after hibernation*	*before hibernation*	*males*	*females*	*sex ratio*	*total number*
1964	15–17	20–25	21–28	32–40	47.4	47.2	0.64	283
1965	15–19	27–32	23–24	———	46.8	47.2	0.62	260
1966	15–19	26–34	25–31	>40	44.5	48.2	0.45	49
1967	———	———	25–33	———	49.7	48.6	0.95	144
1968	16–18	27–32	25–31	>40	47.7	48.3	0.65	599

2. *Growth*

First year frogs increased in length from about 17 mm to 30 mm, with the exception of 1964: in that year the increase was only from 16 to 23 mm. Usually second year frogs can reach at the end of the year a length of more than 40 mm. In 1964, however, their growth was retarded as well and they did not exceed 40 mm. The retardation of growth in 1964 has to be ascribed to the dry summer with high evaporation (see Table IV). We may assume that this retardation was caused by the long period of dryness during which animals stay in hiding-places and feeding activity is low.

It was not possible to gain information on the growth of the adults.

TABLE IV

Evaporation in mm according to the method of Penman*. The "normal" value of the average evaporation per month is the average of the figures found for the period 1931–1960. Data have been obtained from reports of the K.N.M.I.

Month	*Normal*	*Deviation in*			
		1964	*1965*	*1966*	*1968*
June	124	+ 8	− 9	−16	−11
July	116	+14	−25	+17	− 2
August	97	+ 5	− 8	− 4	−18
September	59	+12	− 3	− 2	− 3

* In this method the combined effect of temperature, wind velocity and radiation is recorded.

C. *Analysis of the results*

1. *Number per month*

For further analysis the data of Fig. 2 are put together per month in Fig. 3. They are separated according to the size of the individuals; specimens longer than 40 mm (Fig. 3a) were mainly captured in spring, a few in summer and a larger number in autumn. As regards the ones that are smaller than 40 mm (Fig. 3b), there was only a maximum in summer.

The peak of adults (Fig. 3a) in spring has to be ascribed to migration to and from breeding-places; this will be demonstrated later (p. 247). In summer the frogs are probably scattered and have mainly feeding activity in a small area; hence, the catches were small. In autumn the yield from the traps increased again. This is presumably connected with the search for suitable sites for hibernation.

Fig. 3b demonstrates that in contrast to the adults, frogs smaller than 40 mm show a peak in June-July. This peak is caused by just metamorphosed animals. At first they stayed some time near the water and were caught by hand, later on they dispersed and were trapped.

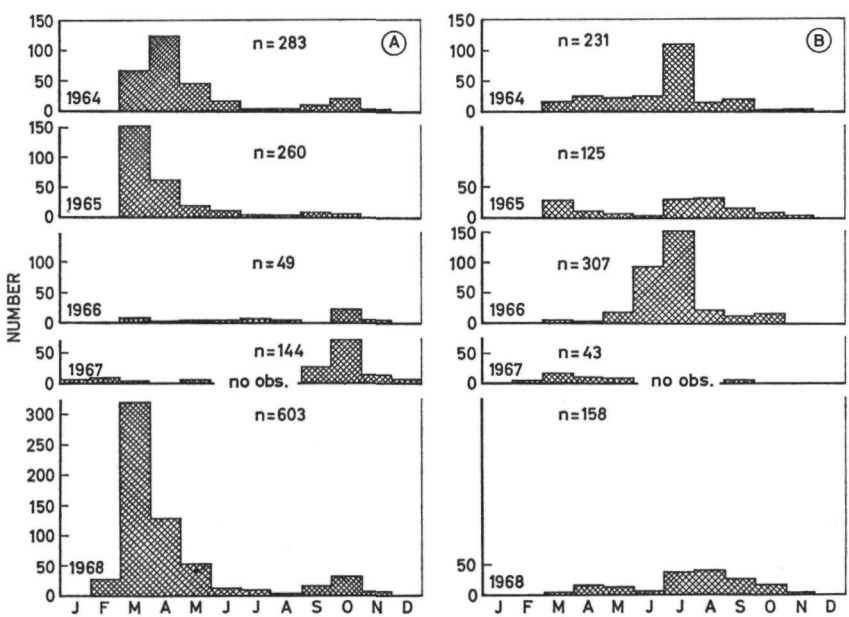

Fig. 3. Number of frogs captured per month. A. Adults (longer than 40 mm). B. Individuals smaller than 40 mm.

Migration of second year frogs could not be proved. Probably a number of them lived in the experimental area and were trapped at feeding activity.

2. *The distribution of the adults in the trapping-square from March to May*

The yield of adults on certain dates in spring is put in relation to the distance to the water. For that purpose the yield of the traps with the same distance to the water (a row of traps) is counted together (Table V). Again the results of 1966 and 1967 could not be used, because of flooding of many traps of the trapping-square.

The yield of the trapping-square enables us to draw conclusions as to the direction of the migration of the adults in spring. For each date of observation the median of the figures of Table V has been calculated and is represented graphically in Fig. 4. The ordinate in this figure represents the distance from the water instead of the row number.

TABLE V

Total number of adults captured per row for each date in spring.

year	*1964*								*1965*							
month	*March*		*April*					*May*	*March*			*April*				*May*
day	*19*	*26*	*2*	*9*	*16*	*23*	*30*	*7*	*17*	*24*	*31*	*7*	*14*	*21*	*28*	*5*
row 5	0	3	0	3	7	2	4	4	4	3	0	0	0	2	1	1
row 4	0	10	0	1	7	4	4	2	4	3	2	0	0	6	1	1
row 3	0	10	0	2	5	3	5	1	5	9	5	0	2	4	2	0
row 2	0	24	0	6	9	11	2	1	6	0	2	2	1	4	2	0
row 1	0	24	7	10	22	4	2	2	8	4	7	2	6	1	1	0
row 1a	–	–	–	–	–	–	–	–	7	12	24	4	1	0	1	0

year	*1968*																
month	*February*	*March*						*April*									*May*
day	*27*	*8*	*15*	*19*	*22*	*26*	*29*	*2*	*5*	*9*	*11*	*16*	*19*	*23*	*26*	*30*	*7*
row 5	5	3	10	9	5	4	2	5	6	1	0	2	1	0	0	2	3
row 4	4	6	6	4	6	11	1	0	1	0	0	1	1	2	1	4	7
row 3	3	8	13	5	3	8	3	3	1	0	1	0	3	2	0	3	0
row 2	4	3	8	5	7	7	3	5	5	2	1	0	3	2	1	4	3
row 1	3	4	8	8	12	35	7	9	4	0	0	1	7	6	2	1	0
row 1a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

In the course of three years of observation a comparable pattern was obtained. As soon as frogs become active and appear in the traps, the median lies about halfway in the trapping-square. In the following dates of observation the median shifts to the water and back again.

The shift of the median in spring can be explained as follows. As the population migrates to the Heerenven, a number of frogs passes

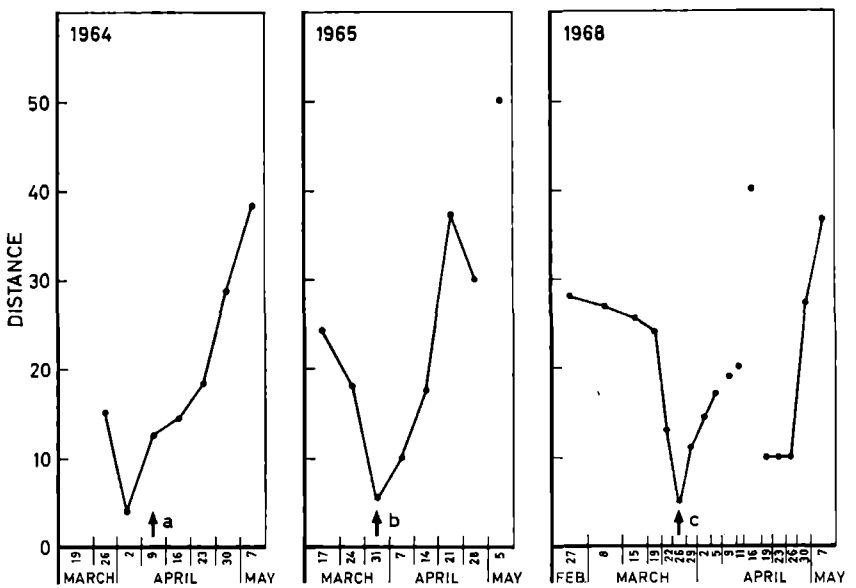

Fig. 4. Distance (in m) from the water of the median of the yield of trapping-square. For calculation of the median, see text. Arrow a.: eggs present; b.: copulation observed; c.: choruses present.

through the trapping-square: then the median has to be expected halfway in the trapping-square. At the time reproduction activity is maximal, the median is expected to be found at the shortest distance from the water. This agrees with direct observations of breeding activity as indicated in Fig. 4 with arrows a, b and c; only after spawning the median shifts away from the water.

There is some irregularity in 1968 in the period of April 9–16, when the number of catches was low. This low number is undoubtedly caused by the prevailing cold weather in that week; in the next days temperatures returned to normal and the migration from the water continued.

3. *Population fluctuation*

As it is not known which percentage of the frogs present in the area had been trapped, no estimation of the population can be made. Yet, something can be said on the fluctuations of the different classes in five years of observation. For this purpose the number per trap, trapped in a particular period, will be compared. For adult and second year frogs the period of March-April-May is suitable. For the youngest generation a period from metamorphosis until the end of the year is considered. As the number of traps in use was not the same each year, it is necessary to compare the yield per trap.

For adult, second year and first year frogs separately the number per trap and per period is added; for each age group the sum for the five years is given the value 100% (see Fig. 5).

a. First year frogs

It appears that the generation of 1966 is the most abundant. In that year the water level was high, the temperature was normal and relative humidity high.

b. Second year frogs

The generation of 1966 causes a peak in the number of second year frogs in 1967. There is also a peak in 1964; preliminary observations (1961–1963) showed that the generation of 1963 was numerous; this is confirmed by the high number of second year animals in 1964.

c. Adults

Nothing can be said about the peak in 1964. In 1965 less adults are trapped than can be expected after the great number of second year frogs in spring 1964. Probably these frogs were strongly affected by the dryness in 1964, resulting in a great mortality. The scarcity of adults in 1966 is in accordance with the low yield of first year frogs in 1964 (again caused by the dryness of 1964 and resulting also in a low number of second year frogs in 1965). The generation of 1965 was apparently too small to bring the number of adults in 1967 up to a higher level. Again there is a peak in 1968; it must be ascribed to the successful generation of 1966.

Apart from these two possible causes affecting the size of the population (dryness in 1964, high water in 1966), nothing can be concluded from our data about other causes of fluctuation of the population, *e.g.*, predators, immigration and emigration.

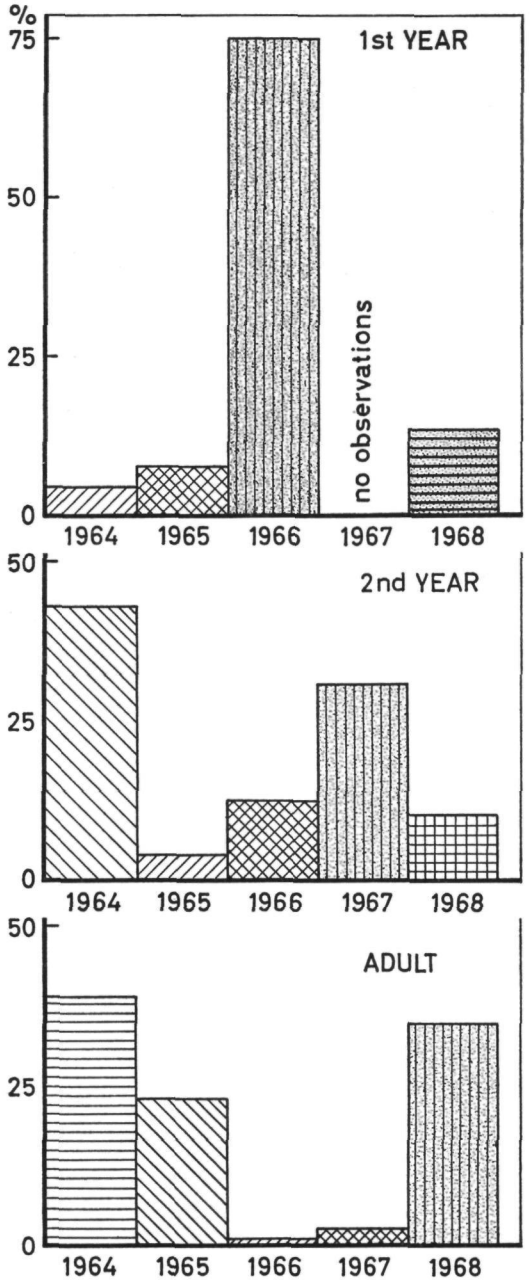

Fig. 5. Number of frogs per trap. First year frogs from metamorphosis to the end of the year; second year and adult frogs from March 1 till May (included). For each age group the sum for the five years is given the value of 100%.

V. DISCUSSION

Trapping of amphibians is not new, but the technique is not widely used. All species of amphibians present in a certain area are trapped. Generally, the yield depends on activity and density of the population and the number and size of the traps. To get information, a sufficient number of traps must be placed in an area where Amphibia occur regularly. Reliability of the results depends on the frequency with which the traps are inspected. To our knowledge systematical trapping has not been practised during a number of years in succession.

During the five years of observation breeding activities were observed within a few days between March 10 and April 7. According to GISLÉN & KAURI (1959) in Sweden spawning usually occurs in the second half of April. In Germany (Frankfurt/Main) spawning has been observed between March 27 and April 7 over a period of three years (1952, 1954 and 1955; see RÜHMEKORF, 1958).

The length of the larval period in Sweden (GISLÉN & KAURI, 1959) is 14 weeks. In the Netherlands it usually amounts to 13–14 weeks. In Sweden first year frogs have a length of 22–24 mm at the end of the year; in the Netherlands they normally reach 26–34 mm. Second year frogs in Sweden measure 37 mm; in the Netherlands they grow over 40 mm. GISLÉN & KAURI mention a 48 mm third year frog. We are not able to separate this class from older specimens. Maximum length of adults in Sweden and in the Netherlands is 69 mm and 65 mm for males and 65 mm and 69 mm for females, respectively. It seems that there is no difference in length between adult *Rana arvalis* from Sweden and from the Netherlands. Nevertheless, compared with the Netherlands, the Swedish young classes grow slowly.

From our investigation it seems that *Rana arvalis* can reach sexual maturity as third year frog, *i.e.*, after the second hibernation. This can be concluded from Fig. 5, in which adults of 1968 mainly represent third year frogs (generation 1966). It can also be concluded from Fig. 2, which makes it clear that in 1964 second year frogs stayed behind in growth; in 1965 they appear in the traps as small third year frogs in relative large numbers. From this it can be concluded that they are involved in the migration. Moreover, in the same spring (1965), individuals of 34 mm and longer were clearly sexually differentiated; the males showing the blue colour and the females carrying eggs.

Considering the fluctuations of the population we have assumed that the number of individuals per trap over a certain period is a parameter of the number of adult, second and first year frogs in this period in the experimental area. We are not sure that the number per trap over a certain period is also a parameter of the population size, as up to now

we know little about emigration, immigration and mortality. Yet we believe that our data give some information about the population fluctuation, since in all year classes we can indicate the influence of the dryness of 1964 and the high water in 1966.

VI. SUMMARY

A population of *Rana arvalis* Nilsson was studied weekly during five subsequent years in the conservation area "de Hamert", which is part of a region of sand dunes covered with heather in the upper parts, and with *Molinia* and *Erica* in the lower parts.

In total 2,203 frogs were trapped mainly in traps which were arranged in a so-called "trapping-square" on the margin of the Heerenven.

Additional direct observations were also made. Breeding choruses and spawning were restricted to a very short period in early spring; in the successive years it could be observed between March 10 and April 2 at temperatures between 4 and 10° C. During two or three days after spawning females showed copulation scars. Depending on the temperature, the larval period lasted 11–15 weeks; normally it took 13–14 weeks. In all the years of observation the entire larval population completed its metamorphosis within one week. The tail of a young frog was resorbed within two days.

At metamorphosis young frogs measured 15–19 mm. At the end of the year, first year frogs normally had a length of 26–34 mm, while second year frogs exceeded 40 mm. Third year individuals were sexually active. Average length of males and females (third years and older ones) was equal (47–48 mm; maxima: 65 mm for males and 69 mm for females). The sex ratio was approximately 0.6.

Adults were trapped mainly in spring; during summer they were obtained in very small numbers; in autumn their number increased again. The great number trapped in spring is due to migration to and from the spawning site; part of them were third year frogs.

As soon as spawning was completed, the frogs left the water if weather conditions were favourable.

In our opinion weather has a great influence upon population size. In 1964 (extremely dry) the population was reduced, whereas in 1966 (a wet year) an increase started.

ACKNOWLEDGEMENTS

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RÜHMEKORF, E., 1958. Beiträge zur Ökologie mitteleuropäischer Salientia. I. Abhängigkeit der Laichabgabe von Aussenfaktoren.—Z. Morph. Ökol. Tiere **47**: 1–19.

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STELLINGEN

I

Waarnemingen aan populaties van amfibieën gedurende weinig jaren geven een onvolledig beeld van die populaties.

Dit proefschrift

II

Juszczyk (1951) neemt ten onrechte aan dat hij slechts door toeval geen migratie observeerde bij Rana esculenta tijdens de voortplantingsperiode.

W. Juszczyk, 1951. The migration of the aquatic frog Rana esculenta. L.Bull. Intern.Acad.Pol. ser B II 342-369
Dit proefschrift

III

De theorie van Berger (1973) over 'Rana esculenta Complex' wordt onvoldoende gesteund door waarnemingen elders uit het areaal van Rana esculenta.

L. Berger, 1973. Systematics and Hybridization in European Green frogs of Rana esculenta Complex. J. of Herpetol. 7, 1-10

IV

Het waarnemen door Wahl (1969) van drie formanten met constante frequenties in de koorroep van Rana esculenta kan berusten op een fout in zijn methodiek.

M. Wahl, 1969. Bio-akustiek des Wasserfrosches Rana esculenta. Oecologia 3, 14-55

V

De term 'Optimaal milieu' betrokken op plantensoorten dient niet gerelateerd te worden aan de maximale produktie van de betreffende soorten.

G. Londo, 1971. Patroon en Proces in duinvalleivegetaties langs een gegraven meer in de Kennemerduinen. Diss. Nijmegen.

VI

Het is onwaarschijnlijk dat alle door Linskens (1966) gebruikte voortplantingscellen van benthische algen in het stadium zijn waarin ze zich vasthechten.

H.F. Linskens, 1966. Adhäsion von Fortpflanzungszellen benthontischer Algen. Planta 68, 99-110

VII

Er is onvoldoende evidentie om aan te nemen dat de door Barbieri en Oterino (1972) aangetoonde diffundeerbare factor uit het gelei van Bufo-eieren een wezenlijke rol speelt bij de bevruchting van die eieren.

F.D. Barbieri en J.M. Oterino, 1972. A study of the diffusible factor released by the jelly of the egg of the toad Bufo arenarum. Development Growth and Differentiation 14, 107-117

VIII

De bewering van Schmidt en Enigk (1972) dat de door hen gevonden intensiteit van besmetting met de longnematode Rhabdias bufonis en de stekelsnuitworm Acanthocephalus ranae binnen een populatie van Bufo bufo verantwoordelijk is voor de grote sterfte in deze populatie moet als onjuist worden aangemerkt.

U. Schmidt en K. Enigk, 1972. Ungewöhnlich starker Helminthenbefall bei Erdkröten. Deutsche Tierärztliche Wochenschrift 79, 625-626

IX

Het vinden en gebruiken van schone energie is een absolute voorwaarde voor het voortbestaan van de huidige westerse samenlevingsvorm.

H.T. Odum, 1971. Environment, Power and Society. Wiley-interscience

X

Aangezien reizen bij oecologisch onderzoek meestal noodzakelijk is (dit proefschrift) dienen ook voor studenten de daaraan verbonden kosten door de universiteit te kunnen worden vergoed.

XI

Bij het vaststellen van de zendtijd voor televisie dient men rekening te houden met de invloed van dit medium op de gemeenschapszin van de mensen.

XII

Iedere gelijkenis tussen een promotieplechtigheid en een hoogmis is louter toevallig.

Nijmegen, 21 september 1973 J.J. van Gelder